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ON THE SYSTEMATIC POSITION OF AMPHIZOIDAE,  
EMPHASIZING FEATURES OF THE FEMALE GENITAL ORGANS  
(INSECTA: COLEOPTERA: ADEPHAGA)

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ABSTRACT

*Amphizoidae have been considered a group of adephagan beetles phylogenetically situated between the Ge- and Hydradephaga. Study of structure of larvae, metathorax of adults and female genitalia, particularly the ovipositor, demonstrates that this family belongs within the Hydradephaga. Monophyly of the group comprising Amphizoidae, Hygrobiidae and Dytiscidae, is compared with results of other phylogenetic investigations. Autapomorphies of members of Amphizoa and especially of the female genitalia of Amphizoa lecontei are compared with those of other members of Hydradephaga.*

ZUSAMMENFASSUNG

*Die artenarme Familie der Amphizoidae wurde bisher systematisch zwischen die Ge- und Hydradephaga eingereiht. Untersuchungen zur Morphologie der Larven, des Metathorax der Imagines und des weiblichen Genitalapparates insbesondere des Ovipositors zeigen, daß diese Familie phylogenetisch zu den Hydradephaga gehört. Nach diesen vergleichenden Untersuchungen sind Amphizoidae, Hygrobiidae und Dytiscidae monophyletisch und die Amphizoidae stehen den beiden anderen Familien als Schwestergruppe gegenüber. Ergebnisse anderer systematischer und phylogenetischer Untersuchungen werden mit dieser These in Beziehung gesetzt und verglichen. Die Autapomorphien der Arten der Gattung Amphizoa im Besonderen die weiblichen Genitalorgane und Anhänge von Amphizoa lecontei werden mit denen anderer Vertreter der Hydradephaga verglichen.*

INTRODUCTION

Aspects of phylogenetic relationships of the six families of Hydradephaga (Amphizoidae, Dytiscidae, Gyrinidae, Haliplidae, Hygrobiidae and Gyrinidae), the relationship of Hydradephaga to Geadephaga, and the relationship of Trachypachidae to both subdivisions of Adepaga have been examined by Bell (1966, 1982), Forsyth (1968, 1970), Crowson (1975, 1981), Burmeister (1976, 1980), Dettner (1979), Roughley (1981), Evans (1985), Baehr (1979), Hammond (1979), Ward (1979), Ruhnau and Brancucci (1984), Kavanaugh (1986), Ruhnau (1986), Beutel and Belkaceme (1986) and Beutel and Roughley (1988).

A common result of most of these studies is that Hygrobiidae, Dytiscidae and possibly Amphizoidae belong to a monophyletic unit (e.g., Burmeister 1976, 1980). The relationship of the remaining families to this group and to each other is more controversial.

These studies may be characterized collectively by study of a wide variety of structural, chemical and histological features of adults (as well as some features of larvae and pupae), and all discuss the systematic position of Amphizoidae at least in part. The purpose of the present study is to examine the systematic position of Amphizoidae by synthesizing all of the available information and using the character states in a cladistic analysis.

The ovipositor of Hydradephaga possesses a number of functional character systems useful for phylogenetic reconstruction. These character systems were studied for most Hydradephaga by Burmeister (1976, 1980) although a detailed study of Amphizoidae was not presented there. Therefore, in the present study a more detailed description of the female organs includes muscular features and functional considerations. This is used for placement of Amphizoidae within Hydradephaga and supplementary characters are taken from the literature to ascertain whether or not they support this hypothesis.

## MATERIALS AND METHODS

### List of species examined (adults)

Amphizoidae — *Amphizoa insolens* LeConte, *A. lecontei* Matthews.

Hygrobiidae — *Hygrobia tarda* (Herbst), *H. nigra* (Clark), *H. australasiae* (Clark).

(Dytiscidae: Copelatinae) — *Copelatus atriceps* Sharp, *C. haemorrhoidalis* (Fabricius).

Dytiscidae: Colymbetinae: Agabini — *Hydronebrius cordaticollis* (Reitter), *Agabus bipustulatus* (Linnaeus), *Platambus maculatus* (Linnaeus).

Dytiscidae: Colymbetinae: Colymbetini — *Rhantus pulverosus* (Stephens).

Noteridae — *Noterus clavicornis* (DeGeer).

Halipilidae — *Halipilus lineaticollis* Marsham.

Gyrinidae — *Gyrinus substriatus* Stephens.

Only dried specimens of *Hydronebrius* were available. All other specimens were preserved in FAE or in 80% ethanol prior to dissection. Drawings show internal skeletal structures, internal genital organs and the musculature systems, but other internal organs are omitted.

The names of sclerites, internal organs and muscles are based on the ground plan of female genitalia of Adephegata developed by Bilz (1976) and Burmeister (1976, 1980).

Apomorphies of the ovipositor of amphizoids and their relatives can be used to refine the reconstructed phylogeny of Hydradephaga proposed by Burmeister (1976). For families such as Amphizoidae and Hygrobiidae analysis is easier because each contains only a single genus.

Among Hydradephaga, members of Dytiscidae are the most difficult to characterize in terms of a ground plan. This is in part because Dytiscidae is the most diverse family of Adephegata and because the form and function of various structures of the female genitalia, in particular, has been altered during the development of various mechanisms of oviposition and copulation (Burmeister 1980).

The current classification of Dytiscidae suggests seven subfamilies: Copelatinae, Colymbetinae, Hydrporinae, Laccophilinae, Agabetinae, Dytiscinae and Aubehydrinae. Not all authors would agree with the limits and composition of these subfamilies and Aubehydrinae are excluded from this discussion because I have not dissected specimens of the single included species.

Burmeister (1976) suggested that *Copelatus* Erichson (Copelatinae) is the sister group to the remaining Dytiscidae. This phylogenetic position for

copelatines is suggested also by studies of larval and pupal structure (Ruhnau and Bruncucci 1984, Bruncucci and Ruhnau 1985, Ruhnau 1986). Among the remaining subfamilies of Dytiscidae, phylogenetic relationships are more problematic. For instance, Colymbetinae is a stage group and is not monophyletic (Burmeister 1976). However, among "colymbetines", members of Agabini and Colymbetini form a monophyletic group and are probably the sister group of the remaining groups (Burmeister 1976) although representatives of some tribes and many genera were not examined. This phylogenetic position is also suggested by study of larval and pupal characters (see above). Members of Hydroporinae, Dytiscinae and Laccophilinae + Agabetinae form well defined monophyletic groups but their relationships to each other are difficult to assess (Burmeister 1976, in press). In part, this latter is due to reductions and specializations due to mode of oviposition, body size, etc.

The method for deducing synapomorphies of Dytiscidae was to develop a ground plan of dytiscid structure based on features of Copelatinae which were compared to those found in Agabini + Colymbetini. Derived features of these groups were taken as synapomorphies of Dytiscidae. This method was used extensively with features of the female ovipositor but also with other character states from other character systems.

In general, for phylogenetic analysis I reject apomorphic characters expressed only as character reductions or losses. Such characters provide supplementary information only if supported by a wealth of character gains. All characters are polarized as primitive (plesiomorphic) or derived (apomorphic) according to the methods of phylogenetic systematics of Hennig (1950, 1963, 1965, 1981).

## STRUCTURE OF THE OVIPOSITOR

### Internal skeletal structures

For *Amphizoa lencontei* Matthews, the structure of the terminal segments of the female abdomen, including the ovipositor, was first described by Edwards (1951). I use the terms and abbreviations of Burmeister (1976, 1980); however, to facilitate comparison a list of equivalent terms to those used by Edwards (1951) is as follows:

Sternum 8 = gonocoxasterna (CS), anal orifice = end of gut (Ed), coxite with terminal tuft of bristles = gonacoxa (GC), sternum 10 = genital appendages of segment VIII (GH VIII), genital pore = vaginal opening (m Va), valvifer, dorsal part - paraproct = lateral clasp of tergum IX (T IX). In addition, the proctiger of Edwards (1951) may be equivalent to my opening of the bursa copulatrix (Mbc); However, homology of these is not certain.

The amphizoid ovipositor belongs to the sensitive, touching type: gonocoxae (gonocoxites) are elongated and possess some apical bristles (Fig. 2). Edwards (1951, plate 3) illustrated the last segments in a hyperextended position. While these figures show general structures, they suggest that lateral tergites IX (valvifers) have lost contact with tergite VIII. This is not so because of the function of these segments. During oviposition, the dorsal portion of tergum IX is shifted proximally and the ventral portion is shifted distally which pushes tergite VIII which in turn is articulated with the gonocoxae. This functional complex operates in a similar manner among all Hydradephaga (Burmeister 1980).

The gonocoxosternites (coxosternites VIII) are not in contact ventrally. They are positioned laterally and are heavily sclerotized. When extended (Figs. 3,4), the posterior extensions of tergum IX are shifted laterally whereas when the

ovipositor is retracted they are shifted medially. The ventral view provided by Edwards (1951) shows a sclerite (which he called sternite X) which is situated dorsal to the gonocoxae and which is fused medially. Comparison with the ovipositor of other members of Adephaga and with the hypothetical ground plan of the ovipositor, shows that this sclerite which surrounds the orifice of the vagina (genital pore) is homologous with the genital appendages of Burmeister (1976).

Distally, sclerotized plates enclose ventrally a small slit. In this slit is the papilla of the vagina, which can be fully extended distally. Different species of *Amphizoa* show some differences in form of gonocoxae. Genital appendages VIII cannot be shifted into a distal position as in other groups of Hydradephaga and females can deflex the apex only a little bit to extend the vaginal papilla.

### Internal genital organs of *A. lecontei*

Burmeister (1976) suspected that female members of Amphizoidae, like those of Hygrobiidae and Dytiscidae, have a double genital pore (secondarily reduced to a single pore among females of the subfamily Dytiscinae), because the female genitalia of Amphizoidae, as demonstrated by Edwards (1951), shows affinities to those of *Hygrobia* Latreille and to the ground plan of Dytiscidae. The present study verifies presence of two separate genital openings: vagina and bursa copulatrix. The vagina (Va, Figs. 2, 4c, 5a) is ventral to the bursa copulatrix and is distinctly separate from it. Among noterids and primitive carabids there is a single external opening of the vagina and bursa copulatrix (Fig. 16 of Burmeister 1976). The bursa copulatrix opens into a membranous sac with its external aperture between the basal parts of the gonocoxae (bc, Figs. 2, 5a). After copulation, this reservoir is filled by the spermatophore and is expanded. The ductus receptaculi originates in the ventral area of the proximal part of the bursa. This tube-like ductus is thickened and surrounded by glandular epithelium (apomorphic character?), in contrast to that of all other Hydradephaga. The ductus receptaculi has a process which projects from the distal curve of the vagina (Figs. 4c, 5a); this tube contacts the mouth of the long receptaculum seminis, which is the reservoir for sperm. This reservoir is situated beneath the distal part of the bursa. The ductus seminalis, the tube for sperm transport into the vagina, is very short. A circular muscle can close the median oviduct, anterior to the opening of the ductus seminalis into the vagina (autapomorphic state of Amphizoidae?). The expansion of the receptaculum depends on the physiological condition of the female after or before copulation or oviposition.

A small, rounded, clasp-like sclerite is present on either side of the bursa copulatrix in *A. lecontei* (SK, Fig. 5a). Two small sclerites are present in the lateral wall surrounding the opening of the bursa copulatrix. These sclerites are different from sclerotizations of the bursal wall that are found among Carabidae and some Dytiscidae; most members of these groups possess sclerotized areas (bursal sclerites, Burmeister 1980) in the ventral or proximal areas of the bursa which are contacted by the aedeagus and spermatophore during copulation. In most members of Agabini (Dytiscidae) there is a ventral sclerite with insertion of muscle between bursa and vagina; in female specimens of *Hydronebrius* Jakowlew (Fig. 5, 6) (Agabini), a sclerotized area is not evident, but the bursa and vagina are connected by surrounding musculature (Fig. 5d).

### Arrangement of ductus receptaculi and ductus seminalis

The ductus receptaculi and ductus seminalis are tubes for transport of sperm to and from the receptaculum seminis and to and from the vagina. The ductus seminalis (Ds) extends from the receptaculum seminis (rs) and opens into the vagina (Va) posterior to the median oviduct (Od). The ductus receptaculi (Dr) extends from the bursa copulatrix (bc) to the receptaculum seminis (Fig. 5). The differing arrangements of these ducts suggests that they have phylogenetic value. Among females of Carabidae, Dytiscidae and Hygrobiidae the ductus receptaculi opens ventrally into the bursa copulatrix (Fig. 5b,c,d) and therefore the origin of the ductus receptaculi is distinctly posterior of the proximal end of the bursa copulatrix (Fig. 5a) and this is a feature unique to Amphizoidae among all Adephaga which have been studied.

The relative lengths and positions of these ducts and associated organs is important also. Females of *Amphizoa* LeConte (Fig. 5a) have the receptaculum seminis located beneath the bursa copulatrix and therefore the ductus receptaculi is moderately short whereas the ductus seminalis is very short. In addition both ducts are distinctly separated from each other throughout most of their lengths.

Females of *Hygrobia tarda* (Hygrobiidae, Fig. 5b) have the receptaculum seminis isolated from the bursa copulatrix, the ductus receptaculi and ductus seminalis are elongated and they are connected throughout much of their length. A unique feature of *Hygrobia* is the presence of an accessory gland located at the proximal end of the bursa copulatrix (Figs. 5b, 9). This character was observed in specimens of both *H. nigra* and *H. tarda*.

The arrangement among members of Dytiscidae is less straightforward. Among Dytiscidae, the ductus receptaculi are much thinner than the ductus seminalis which is the inverse of the size ratio of ducts in *Hygrobia* (Figs. 5b to 5c,d). In females of most taxa the ductus receptaculi and ductus seminalis are elongate, separated ducts (Fig. 5b) leading to and from an isolated receptaculum seminis. This ground plan for the family Dytiscidae is exemplified by *Copelatus* (Fig. 5c)<sup>1</sup>

Among females of Agabini of Colymbetinae and Dytiscinae, however, the ductus seminalis and ductus receptaculum are connected throughout most of their length (e.g., *Hydronebrius* Agabini, Fig. 5d). Therefore this state in these otherwise derived and phylogenetically separate taxa (Agabini, and Dytiscinae) is probably due to convergence.

### Selected muscular features of *Amphizoa* in comparison with conditions in other Adephaga

Most muscles of the female genitalia of *Amphizoa* can be homologized with those of the ground plan of Hydradephaga (Burmeister 1976, 1980). This is more straightforward for muscles of the genital appendages. For other muscles it is easiest to establish homology to the muscles of Hygrobiidae and Dytiscidae first and then by extension to the ground plan. This is because other hydradephagan groups show differing alterations of musculature associated with specialization in copulation and oviposition. Analysis of the ground plan of Hydradephaga allows comparison to Geadephaga and extrapolation to the ground plan of all Adephaga (Burmeister 1976, 1980).

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<sup>1</sup>Ordish (1966, 1985) has figured females of the austral species *Copelatus australis* (Clark) with a very large vagina and very small bursa copulatrix. This is the opposite situation to that which I have found from study of European species, *C. atriceps* and *C. haemorroidalis*. I suspect that the specimen figured by Ordish is a subadult.

Most of the muscles of the last segments and the female genitalia, and especially those of the genital appendages (gonocoxae and genital appendages VIII, see Figs. 2, 3, 7, 8, 9) are described by Burmeister (1976, 1980) and are not redescribed here. Study of further specimens and of better preserved specimens of *Amphizoa* has allowed a more detailed study of these muscles and a few of these are reported below. The muscle numbers follow Burmeister (1976).

In *Amphizoa* two retractors (M4, M5, Figs. 2-4) of the coxosternum (=coxosternite) originate from the proximal portion of sternum VII, as in many members of Dytiscidae and Carabidae. The protractor muscle (M15, Figs. 2-4) is divided into two components, as in *Hygrobia* (Fig. 9). Among Dytiscidae (but excluding Copelatini and Agabetini) another muscle (M14) also acts as a depressor of tergum IX (Figs 7, 8). As in carabids, gyrrinids and hygrobids, amphizoids have two dorsal retractors (M18, M19) originating at the proximal edge of tergum VIII and inserting distally at the dorsal part of tergum IX and at the dorsodistal membranous area (Figs. 2, 3).

The depressor of the gonocoxae (M27) originates from the coxosternum. It is divided into two bundles dorsoproximally (Fig. 3). The other gonocoxal depressor (M32) is also divided into two components and originates from below the levator (M33) in the ventral area of the lateral portions of tergum IX (Fig. 3). The origin of M32 below M33 is unique among all Hydradephaga studied so far. The two portions of M32 share a single insertion on the gonocoxa. As a result of the arrangement of gonocoxal muscles, the genital appendages can not be extended very markedly nor can they move very far distally.

The parameres and median lobe (= penis) of the aedeagus of males of *Amphizoa* are elongate to accommodate contact with gonocoxae and the inner part of the bursa copulatrix during copulation. The dorsal membranous area above the opening of the bursa is lifted by the strong elevator muscle (M22, Figs. 3, 4). Among carabids, hygrobids (Fig. 9) and amphizoids (Fig. 4) there is a muscle (M 24) extending between the distal and proximal parts of tergum IX dorsally. Among carabids this muscle is larger and extends between the relatively separated portions (dorsal and lateral) of tergum IX. Among dytiscids this muscle occurs only in females of *Copelatus* (e.g., compare Figs. 8 and 9). Earlier (Burmeister 1976), I had represented this incorrectly. Therefore the trend among these four families is toward reduction and eventual loss of this muscle as the movement of the ovipositor changes.

Females of *Amphizoa* have a unique muscle among all Hydradephaga examined. This muscle (M55, Fig. 3) originates from the inner part of the gonocoxa near the articulation with the ventrolateral area of tergum IX and inserts onto the lateral wall of the vagina. The function of this muscle is probably to retain the relative positions of genital appendages VIII and the vagina.

### PYGIDIAL DEFENSE GLANDS

The pygidial glands were used as indicators of phylogenetic relationship among hydradephagan groups by Forsyth (1968, 1970); Dettner (1985) considered the systematic value of the chemical substances produced by these glands. Pygidial glands in females of *Hygrobia* and *Amphizoa* are divided into two, separated, and opposing areas. This character could be considered a synapomorphy for these two families. Beutel (1986) considered the non-doubled character state in Dytiscidae as a reduction, and stated that this state is



convergent with that found in other Hydradephaga because there are doubled glands in some dytiscid genera (e.g., *Colymbetes* Clairville, cf. Dettner 1985).

Females of *Hydronebrius* (Colymbetinae: Agabini) have accessory glands with a longitudinal extension of the duct of the gland to the reservoir. This reservoir is surrounded by many small muscles. In females of *Amphizoa* the glandular parts of this defensive system (dg, Fig. 4b) are in the form of two lobes which open by means of a single tube (= collecting channel of Dettner 1985) into the glandular reservoir (gr, Fig. 4b). This tube, in specimens I have examined, is not surrounded by a well-developed epithelial structure as illustrated by Forsyth (1968). A unique feature of Amphizoidae is an elongate muscle (Mg, Fig. 4b) which extends longitudinally from the proximal end of the glandular reservoir to the edge of tergite IX near the opening of the glandular reservoir. Therefore in *Amphizoa*, Mg pulls longitudinally and compresses the glandular reservoir distally. In other Hydradephaga, Mg is a short muscle (e.g., Fig. 8a, *Copelatus*) which pulls transversely.

### THE SYSTEMATIC POSITION OF AMPHIZOIDAE

Below are listed the synapomorphies of Amphizoidae + Hygrobiidae + Dytiscidae, autapomorphies of Amphizoidae, synapomorphies of Hygrobiidae + Dytiscidae, autapomorphies of Hygrobiidae and autapomorphies of Dytiscidae. Characters of the ovipositor, associated internal organs and musculature are denoted by Arabic numerals. Other characters which are from publications are derived from other structural systems and they are listed as letters. For all characters the apomorphic state is given and characters are listed in the order that they appear on Fig. 13.

#### Synapomorphies of Amphizoidae, Hygrobiidae, Dytiscidae

The connection among these three families is demonstrated by Burmeister (1976), and subsequent studies by Ruhnau (1986) and Beutel and Roughley (1988) agree with this phylogenetic interpretation.

1. Bursa copulatrix and vagina separated; two genital openings between the genital appendages of females (Burmeister, 1976).
2. Genital appendages of segment VIII fused ventrally and, in the resting position, forming a cavity that contains the vaginal papilla.
3. Muscles of genital appendages of segments VIII and IX divided into those that contact the sclerites, and those that are separated by bursal and vaginal muscles.
4. Levator and extensor muscles of genital appendages VIII, which originate at the inner part of the gonocoxa and insert at the anterodorsal edge of the appendages (M 36). These muscles are absent from members of Carabidae examined by Bils (1976).
5. Separation of ductus receptaculi and ductus seminalis.

The arrangement of the gonocoxal depressor (M27) (which originates from the anterodorsal edge of the gonocoxosternum, and inserts at the anterior gonocoxal apodeme near the insertion of M32, the depressor of tergum IX) is similar to that found in most members of Carabidae.

- a. Specialization of pygidial defense glands, which are divided into two sections (Forsyth 1968, 1970; Dettner 1985).
- b. Tergoapodemal ring (Hieke 1966) of segment IX (tergal region) in male genitalia interrupted (Beutel 1986).

- c. Ruhнау (1986) listed larval and pupal synapomorphies of Amphizoidae + Hygrobiidae + Dytiscidae. These are not repeated here.

### Autapomorphies of Amphizoidae

Conclusions presented here are based on study of a limited number of species. Specimens of *Amphizoa davidi* Lucas, *A. carinata* Edwards and *A. striata* Van Dyke have not been studied. Nevertheless from the specimens examined the following synapomorphies seem appropriate.

6. Origin of protractor of bursa copulatrix (M43) inside the gonocoxa near the articulation with the lateral part of tergum IX and at the anterodorsal edge.
7. Origin of dilator of bursa copulatrix (M44) directly under the articulation of tergum IX and gonocoxa and inside the gonocoxa. This character state is related to structure of the bursa, which is fixed between the gonocoxae, and its opening can be moved distally during copulation.
8. A small, newly acquired muscle, the elevator of the vagina (M55), present between M43 and M44. It is undetermined from which muscle system this is derived; possible sources are from those of the gonocoxa, or from either of the independent systems of the bursa or vagina.
9. Presence of a separate depressor of the gonocoxa (M 27b), with origin at the anterior edge of the coxosternum, between M27a and M28.
10. Origin of the depressor of the gonocoxa (M 32) at the inner part of the ventrolateral area of tergum IX, displaced from the anterodorsal edge of the tergite. The origin is double whereas in other taxa the insertion is double (e.g., *Agabus* Leach, Burmeister 1976).
11. Ductus receptaculi with origin at the proximal end of bursa copulatrix (Fig. 5).
12. Bursa copulatrix with two lateral sclerites in the area of the opening (Fig. 5).
13. Position of receptaculum seminis shifted from the anterior area of the bursa copulatrix to near the opening of the median oviduct into the muscular vagina. The ductus seminalis is therefore very short.
- d. Clypeus very large (Beutel 1986).
- e. Galea one-segmented (reduction) (Beutel 1986). This derived character state occurs within Gyrinidae also, with the exception of Enhydrinae: Dineutini, where the galea is absent (Hatch 1927, Franciscolo 1979, Horn 1867, 1881). However, in *Spanglerogyrus* Folkerts, the most primitive known gyrid, the galea is two-segmented (Beutel 1986).
- f. Metafurca markedly reduced in size (Beutel 1986).
- g. Gular region very large, prementum not separated and therefore fused with mentum.
- h. Lacinia with two extremely differentiated, functional areas on the inner edges.
- i. Cavity formed by anterolateral area of elytra and epipleura very deep, such that epipleura in this basal area expanded. In some Carabidae and Noteridae there is also a triangular cavity, but in these taxa the epipleurites are surrounded by a border and separated from the dorsal part of elytra; this latter state is therefore not homologous to that found in amphizoids.
- j. Elongate form of Mg (Fig. 4b) of the pygidial defense gland.
- k. The form of wing-folding exhibited by adult Amphizoidae is considered a provisional autapomorphy of this family. Wing-folding in amphizoids encloses the distal one-fifth of the total wing length (Fig.

10). This contrasts with that known for all other Adephaga except those with secondarily reduced wing-length and Rhysodidae (Hammond (1979). This common character state of rhyssodids and amphizoids would be due to convergence.

1. Kavanaugh (1986) characterized amphizoids as semiaquatic passive drifters in terms of life history. It seems that this could be a secondarily derived condition from a state of fully aquatic habits. This is another provisional autapomorphy of amphizoids.

### Synapomorphies of Hygrobiidae and Dytiscidae

The movement of the ovipositor and its functional consequences among groups of Adephaga is discussed by Burmeister (1980). In ground beetles and amphizoids the ovipositor moves primarily in an anterior to posterior direction with little movement in the dorsal-ventral plane. The vaginal opening is shifted ventrally during oviposition, however.

Among the remaining Hydradephaga the amount of dorsal-ventral movement is increased but in different ways. Among noterids + haliplids + gyrids, the elongated appendages of the ovipositor are more moveable due to reduction of the dorsal part of tergum IX (see Fig. 30 of Burmeister 1980). Among hygrobiids + dytiscids tergum IX remains large and the increased mobility is brought about by a shift in position of tergum IX and articulation with the gonocoxae. Thereby tergum IX and the gonocoxae act together as a jackknife to accommodate the greatly elongated gonocoxae (see Figs. 7, 29 and 30 of Burmeister 1980 and Fig. 40 of Burmeister 1976). Members of Hydroporinae are an exception among dytiscids because in this group tergum IX is reduced in size but this is almost certainly a secondary occurrence.

Rearrangement of these sclerites among hygrobiids and dytiscids suggests a change in functional criteria which are interrelated. The following synapomorphies are apparent.

14. Capability for extreme protraction of coxosterna and tergum IX and the genital appendages; protractor muscles very strong; dorsal retractors of the distal part of tergum IX strong and expansible. Articulation of lateral parts of tergum IX and the gonocoxae act as a fulcrum for evagination of ovipositor.
15. Gonocoxosterna ventrally close together in resting position, with genital appendages VIII positioned medially near the anterior edge; depressor of these appendages short and strong (M28) (lost in members of subfamily Dytiscinae). The depressor M28 of Burmeister (1976, 1980) is not homologous with M13 of Bills (1976) in Carabidae.

Beutel (1986:44-46) listed 10 synapomorphies of Hygrobiidae and Dytiscidae. Of these, five are reductions and two are difficult to polarize because similar states occur in a variety of members of Adephaga. Therefore I prefer to use only the synapomorphies which represent character state gains and which are confidently polarized.

- m. Presence of thoracic defensive gland (Forsyth 1968, 1970, Beutel 1986).
- n. Scapus elongated (Beutel 1986).
- o. Contact of prosternal process with metasternum (Baehr 1979, Beutel 1986).
- p. Ruhnau (1986) listed four larval and pupal synapomorphies shared by Hygrobiidae and Dytiscidae.

### Autapomorphies of Hygrobiidae

16. Presence of an accessory gland at the anterior end of the bursa copulatrix (ag, Fig. 9).
17. Ductus seminalis and ductus receptaculi lie close together; the ductus seminalis proximal to the opening in the vagina is attached at the ventral part of the bursa copulatrix, surrounded by a strong system of muscles (Fig. 5).
18. Only one retractor of the coxosternum (M 5); it is enlarged and fanlike at its origin.
19. Retractor of tergum IX (M 18) with two insertions on the dorsal ridge of this sclerite.
  - q. Beutel (1986:43-44) listed 12 apomorphies of *Hygrobia*, which are not repeated here.
  - r. Adult hygrobiids show a unique set of features associated with stridulation (Beutel 1986:44). On the underside of the elytra is a row of teeth (Fig. 11). This file is in the basal 1/5 of the elytra near the suture. It rubs against the sharp edge of sternum VII. No other Hydradephaga are known to use elytra to stridulate.

The wing folding mechanism and contact of the subcubital binding patches (Hammond 1979) or setal patches (Ward 1979) with the inner elytral surface has been discussed as a phylogenetic character (*e.g.*, Kavanaugh 1986). Its absence from hygrobiids is probably a loss associated with stridulation, because stridulation in this group involves the elytral apex. The function of the binding patches among hygrobiids has been assumed by a broad area of the subcosta and radius (Fig. 12) which contacts the prominent, ventral ridge of the elytron.

- s. Chemical components produced by the pygidial defensive glands are quite isolated when compared to those of other Hydradephaga (Dettner 1985:167). Some of these compounds are not known to be produced by any other insects.
- t. Although not discussed specifically by Ruhnau (1986), it is clear that the larvae of *Hygrobia* exhibit a variety of unique character states.

### Autapomorphies of Dytiscidae

20. The muscle M42 in other Hydradephaga, that is extended between the two gonocoxae (contraction), is the dilator of the distal membranous sac, for prolongation of the bursa copulatrix with insertion at the dorsal area of this membranous area.
21. Existence of a depressor of the gonocoxa, originating from the inner part of the halves of tergum IX and inserting at the dorsal part of the sclerotized appendages of segment VIII (M35).

Other apomorphic characteristics of Dytiscidae presented by Beutel (1986) are reductions or are also found in other hydradephagan groups, and are therefore of less significance as evidence for monophyly of Dytiscidae.

- u. Basal constriction of scapus with S-like curvature (Beutel 1986).
- v. Condylus of ventral procoxal joint reduced (Baehner 1979).
- w. Abdominal sternites with median groups (rows) of bristles (Beutel 1986).
- x. Two types of cells in the pygidial defensive glands (Forsyth 1968).
- y. Nine larval and pupal characters, interpreted as synapomorphic for Dytiscidae, were listed by Ruhnau (1986).

## RELATIONSHIPS OF THE FAMILIES OF HYDRADEPHAGA

The ovipositor of *Amphizoa* is rather primitive, compared with that of Hygrobiidae and some Dytiscidae. The sclerites and appendages of segments VIII and IX are more constrained in *Amphizoa* than in other Hydradephaga allowing less movement of parts of genital segments for oviposition and copulation. The most important derived characters of Amphizoidae, Hygrobiidae and Dytiscidae are in the internal genital tubes of females. In these families, there are double genital openings for the bursa copulatrix (between the base of the gonocoxae) and the vagina (opening between the genital appendages VIII); among these families these genital openings are differentiated according to various functions in copulation and oviposition. These derived character states demonstrate the monophyly of a group comprising Amphizoidae + (Hygrobiidae + Dytiscidae).

The fixed appendages between the lateral sclerites of segment VIII (coxosterna) and segment IX (lateral areas of tergum IX) may be a plesiomorphic character state in *Amphizoa*, as in Geadephaga. The fixed position of the genital appendages between the gonocoxae is very important for oviposition in aquatic habitats and has been lost altogether with the sclerotization of the appendages from most carabids and cicindelids (Bils 1976, Burmeister 1976). These appendages close the female genital tube during burrowing movement of the gonocoxae. In the course of evolution within Hydradephaga these appendages function in testing substrate before egg-laying; during probing, the ovipositor moves from a lateral to a distal position and therefore the gonocoxae are markedly sclerotized and elongate. This tendency is seen in members of *Trachypachus* Motschulsky and *Amphizoa*. This adaptation is more fully expressed among Hygrobiidae and Dytiscidae, in which the dorsally separated lateral sclerites of tergum IX are very strong, especially in its articulation with the gonocoxa, which is its center of rotation.

Among Hydradephaga the relationships of other families is less clear. The monophyletic unit of Amphizoidae + (Hygrobiidae + Dytiscidae) is quite convincing [but see Kavanaugh (1986) for a quite different viewpoint]. These three families I will refer to as Dytiscoidea *s.str.* However, the relative position of Trachypachidae, Noteridae, Haliplidae and Gyrinidae is more difficult. Questions about the positions of these families are important for establishing the sister group of Dytiscoidea *s.str.*

Most authors writing about the phylogenetic position of trachypachids (see references above in Introduction) have considered this group as integral to Hydradephaga except for Kavanaugh (1986) who placed them among carabids. Similarly, gyrinids have been placed among the Hydradephaga by most authors but Beutel and Roughley (1988) placed them as the sister group of all other Adephaga. Also for haliplids there are a variety of opinions [*e.g.*, compare Burmeister (1976), Kavanaugh (1986) and Beutel and Roughley (1988)] about phylogenetic position.

This would appear to leave noterids as the sister group of Dytiscoidea *s.str.* Three examples of differing placement of noterids demonstrate that such can not be done confidently yet. Kavanaugh (1986) placed noterids as the sister group of dytiscids only. This was based on the derived state of two characters (12, 16 — Kavanaugh 1986:92-95). Of these, one (Char. 12) is a loss which occurs broadly among other higher taxa of Adephaga. The other (Char. 16) represents an elongation of the metacoxa. This may represent a useful character; on the other

hand, the three states are subjectively divided and it would be more convincing to have other characters to support this hypothesis.

Beutel and Roughley (1988) listed six characters (13-19, 27 — Beutel and Roughley 1988:388-390, 393-395) which support a phylogenetic grouping of Noteridae + Dytiscoidea *s.str.* From the evidence presented above about the monophyly of Dytiscoidea *s.str.* this would suggest that noterids are the sister group of Dytiscoidea *s.str.* However, the evidence for this is not compelling. Of the five characters, three (Chars. 16, 17 and 27) are reductions. Furthermore, two characters (Chars. 15, 19) are weak characters by the authors' own admission. This leaves only one reliable synapomorphy (Char. 13) of the origin of the metafurca from the intercoxal wall.

Ruhnau (1986) placed Noteridae as the sister group of Haliplidae based on seven characters (Chars. 16-22 -- Ruhnau 1986:242-247, 260-261). Of these, four (Chars. 17, 18, 20, 21) are reductions. Therefore three characters suggest a sister group relationship between noterid and haliplids. Unfortunately, Ruhnau (1986) did not list the genera of noterids larvae which were examined. In the text he mentioned only relatively derived taxa and emphasis was placed on *Noterus* Clairville. Beutel and Roughley (1987:1904) pointed out the problems of working with a phylogenetically derived genus and of using that taxon as representative of a family.

In conclusion, there are at least three radically different hypotheses about the phylogenetic position of Noteridae as well as about the relationships and constituents of Hydradephaga. There is no basis for accepting any of these yet as well documented. Comparison among these three hypotheses suggests that much further research is required and I suspect that the final outcome, if a consensus can be reached, may be different from any of the above hypotheses.

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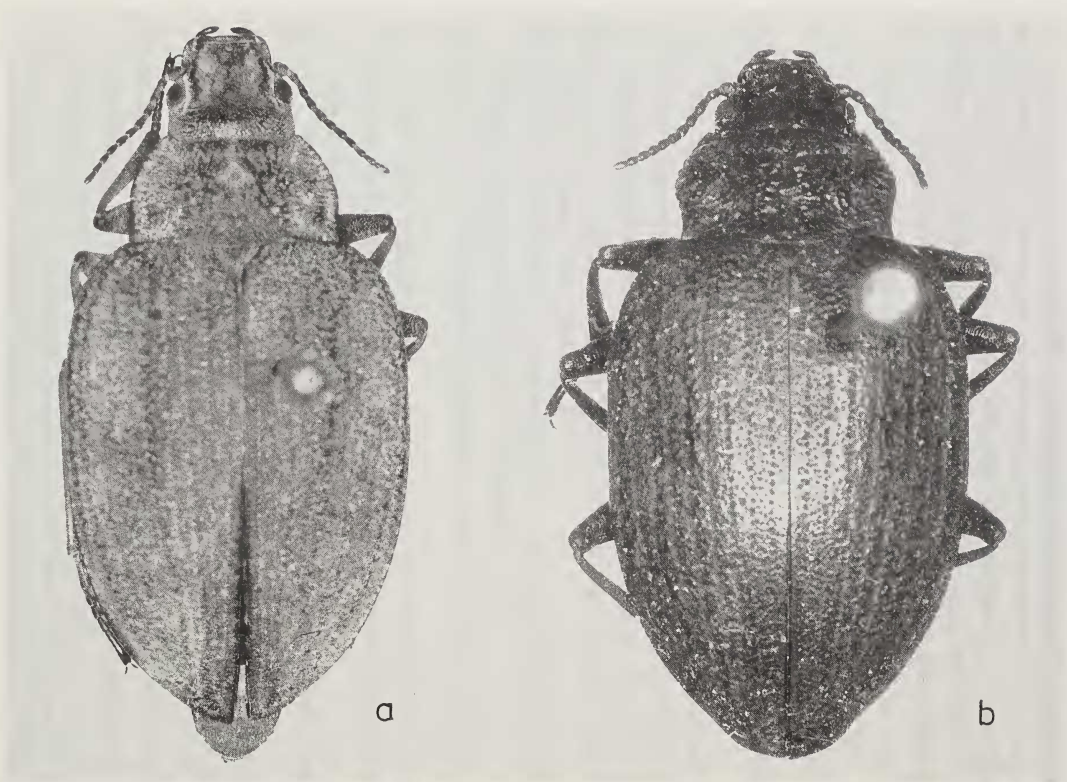


Fig. 1. Dorsal view of Amphizoidae. a. *Amphizoa lecontei* Matthews. b. *Amphizoa insolens* LeConte.

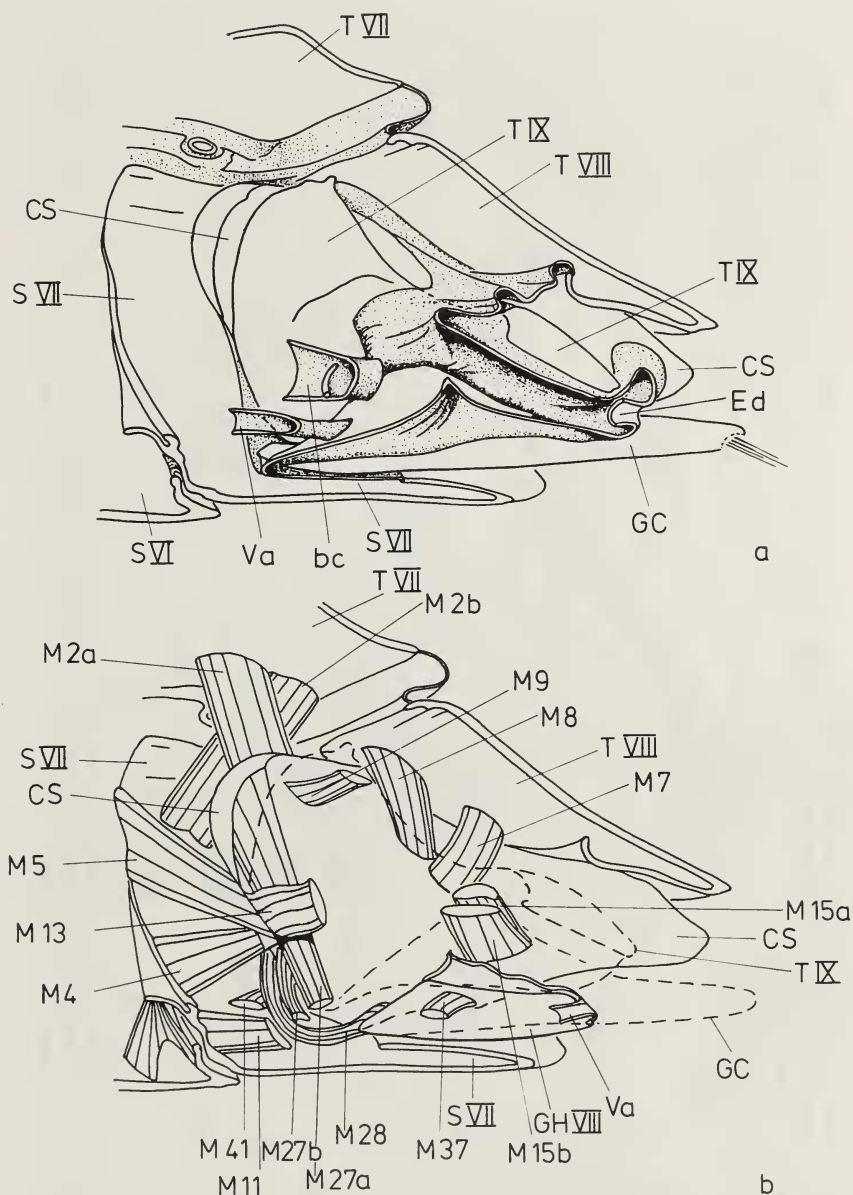


Fig. 2. *Amphizoa lecontei* Matthews, end of abdomen and female genitalia. a. inner view of right side of sclerites and genital ducts, genital appendages VIII removed. b. muscular system of segment VIII, tergum IX and gonocoxa as interrupted lines. Legend: bc - bursa copulatrix; CS - gonocoxosternum; Ed - end of gut; GC - gonocoxa; GH VIII - genital appendages of segment VIII (1. gonapophysis); M - muscular system - muscles - of the abdominal segments and female genitalia; S VI, S VII - sternites of segment VI and VII; T VII, T VIII - tergites of segment VII and VIII; T IX - tergum IX divided in two lateral claspers; Va - vagina.

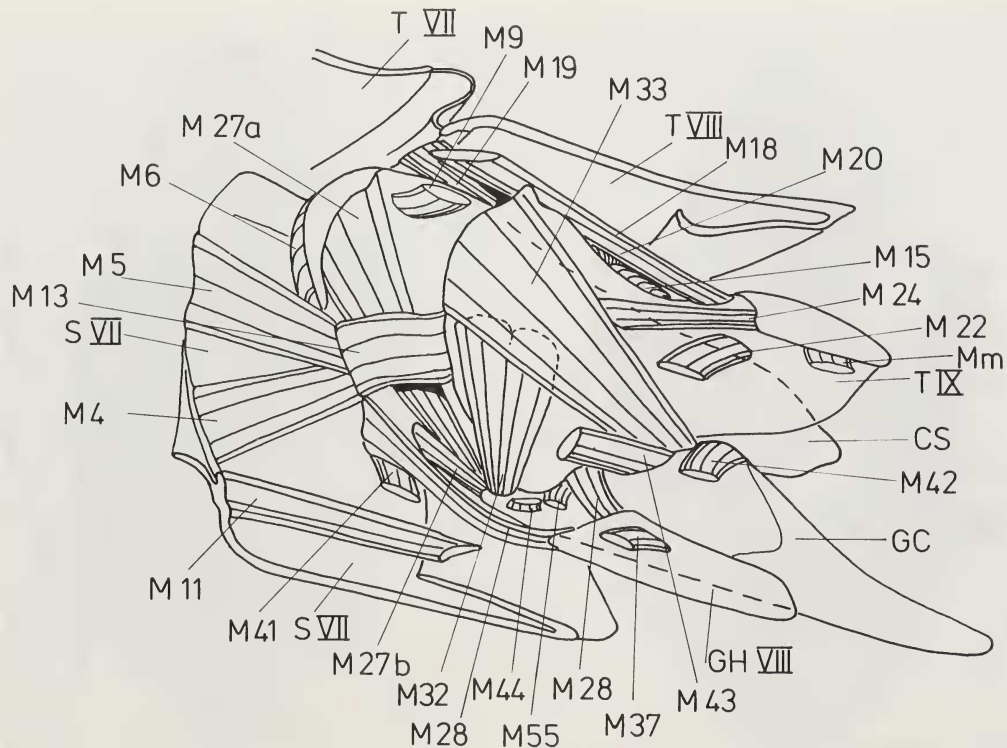


Fig. 3. *Amphizoa lecontei* Matthews, right side of female genitalia, sclerites and muscles. Legend: CS - gonocoxosternum; GC - gonocoxa; GH VIII - genital appendages of segment VIII (1. gonapophysis); M - muscular system - muscles - of the abdominal segments and female genitalia (see text); Mm - muscle of membrane between the halves of tergum IX; S VII - sternum of segment VII; T VII, T VIII - tergites of segment VII and VIII; T IX - tergum IX divided in two lateral claspers.

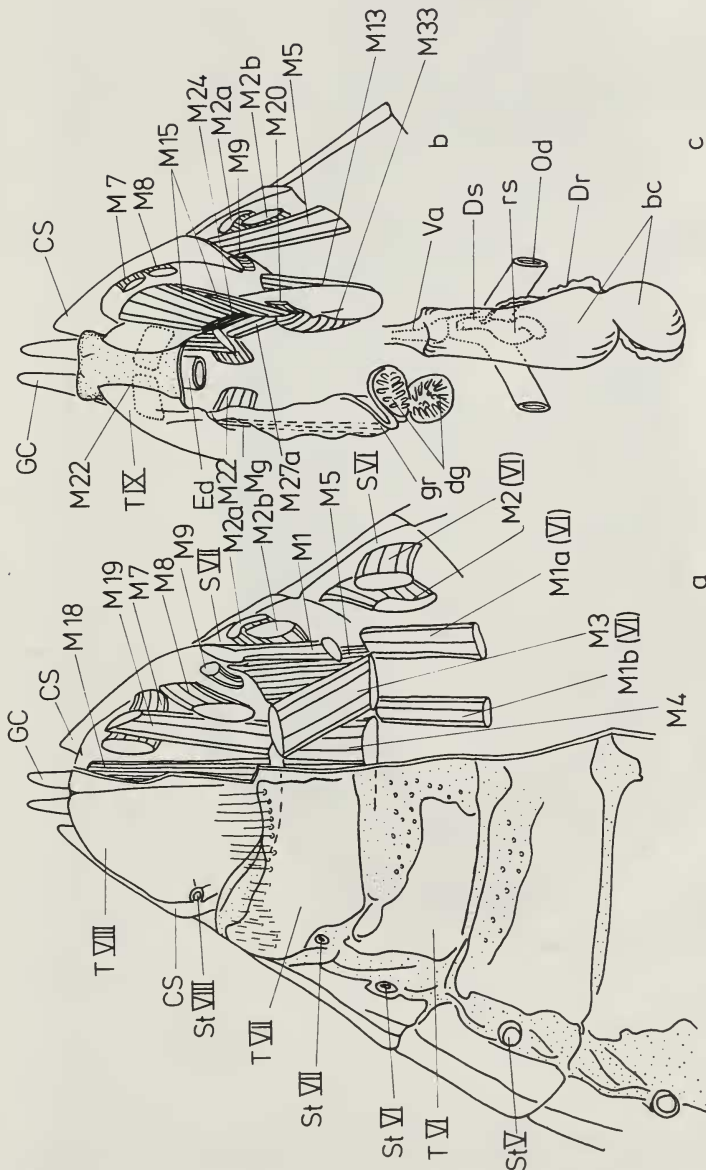


Fig. 4. *Amphizoa insolens* LeConte. a. dorsal view of female genitalia. a. dorsal view of the tip of abdomen and the dorsal muscular system. b. muscular system of the genital appendages and the defense gland. c. inner genital organs. Legend: bc - bursa copulatrix; Cs - gonocoxosterna; dg - defense gland; Dr - ductus receptaculi; Ds - ductus seminalis; Ed - end of gut; GC - gonocoxa; gr - reservoir of defense gland; M - muscular system - muscles - of the abdominal segments and female genitalia; M 1-3 (VI) - segmental muscles of segment VI, same position as muscles M 1-3 in segment VII; Mg - protractor of defense gland; Od - oviduct; S VI, S VII - sternites of segment VI and VII; St V - VIII - stigmata of the segments V to VIII; T VI-T VIII - tergites of segment VI to VIII; T IX - tergum IX divided in two lateral claspers; Va - vagina.

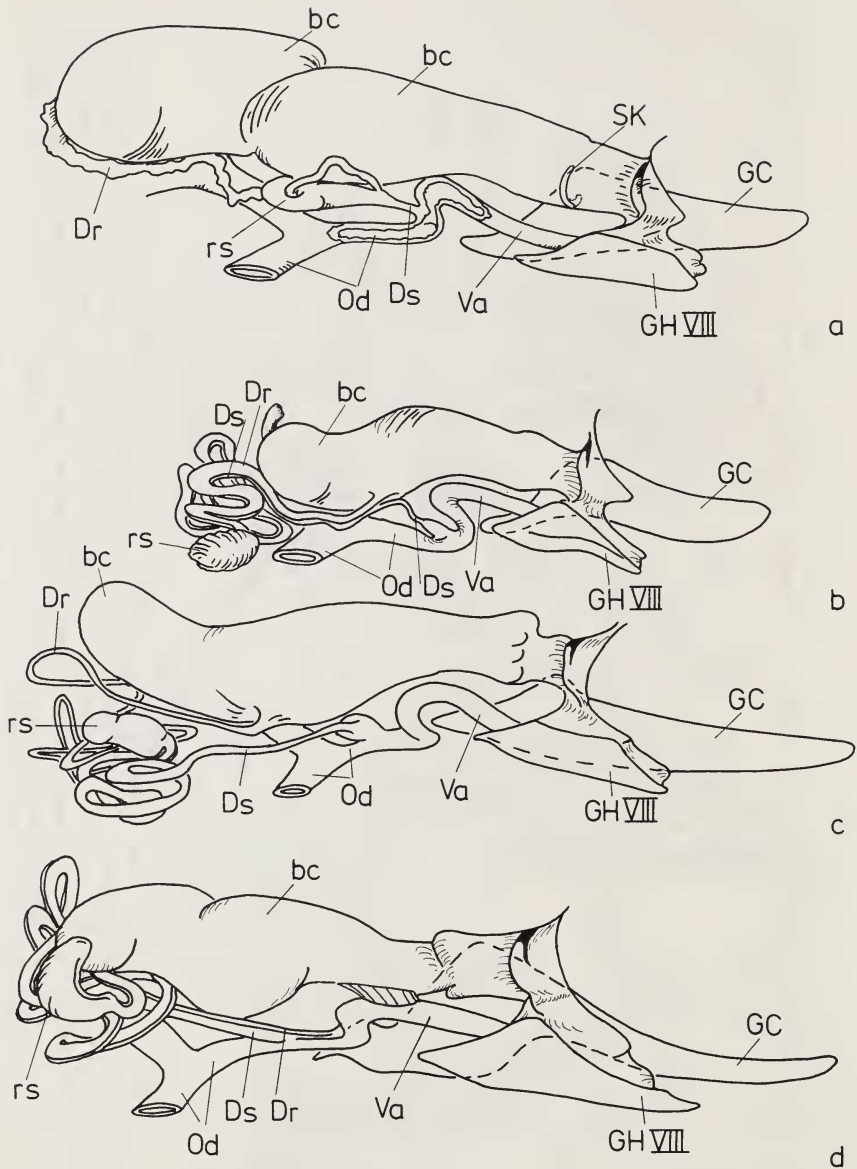


Fig. 5. Inner female genital organs of different species of Hydradephaga. a. *Amphizoa lecontei* Matthews (Amphizoidea). b. *Hygrobia tarda* (Herbst) (Hygrobiidae). c. *Copelatus haemorrhoidalis* (F.) (Dytiscidae, Colymbetinae). d. *Hydronebrius cordaticollis* (Reitter) (Dytiscidae, Colymbetinae). Legend: bc - bursa copulatrix; Dr - ductus receptaculi; Ds - ductus seminalis; GC - gonocoxa; GH VIII - genital appendages of segment VIII (1. gonapophysis); Od - oviduct; rs - receptaculum seminis; Sk - sclerites in the wall of bursa copulatrix; Va - vagina;

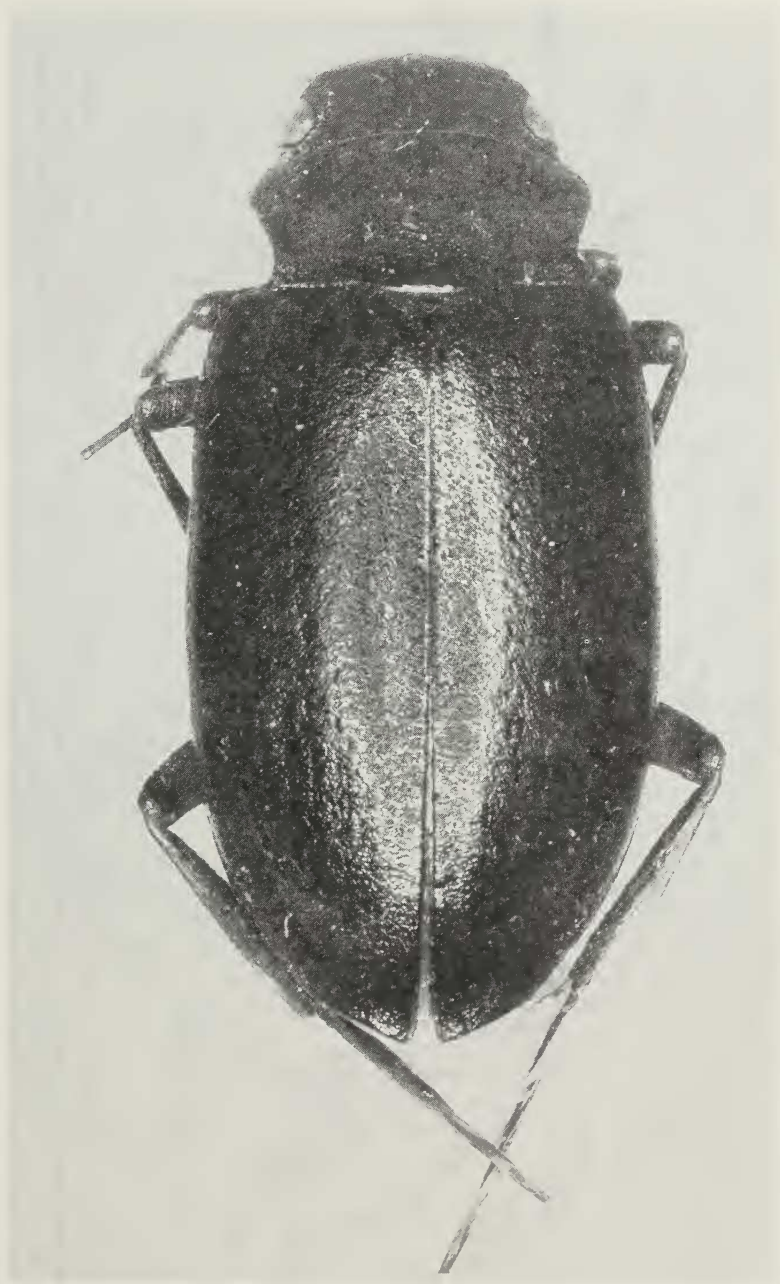


Fig. 6. *Hydronebrius cordaticollis* (Reitter), dorsal view.

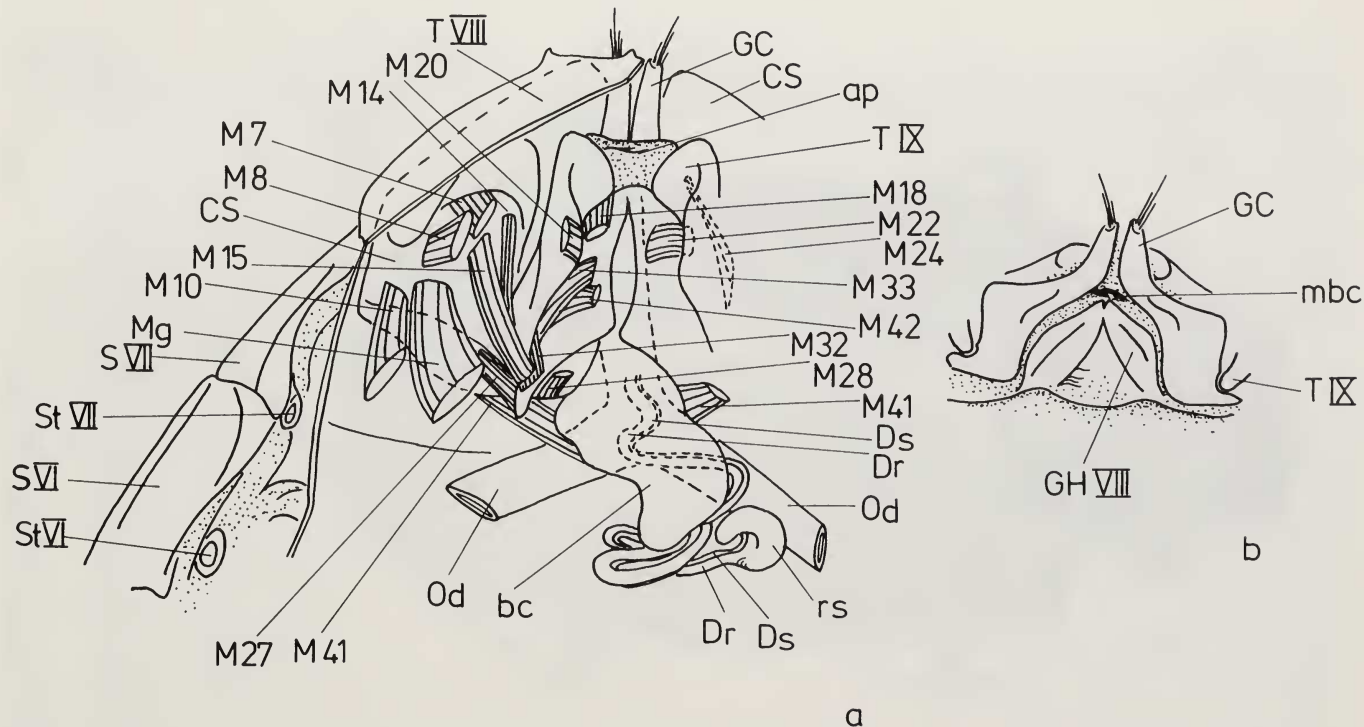


Fig. 7. *Hydronebrius cordaticollis* (Reitter), female genitalia. a. dorsal view of abdomen and muscular system of the genital area and inner genital organs. b. view of the genital appendages. Legend: ap - anal papilla; bc - bursa copulatrix; CS - gonocoxosterna; Dr - ductus receptaculi; Ds - ductus seminalis; GC - gonocoxa; GH VIII - genital appendages of segment VIII (I. gonapophysis); M - muscular system - muscles - of the abdominal segments and female genitalia; mbc - mouth of bursa copulatrix; Od - oviduct; rs - receptaculum seminis; S VI, S VII - sternites of segment VI and VII; T VIII - tergum VIII; T IX - tergum IX divided in two lateral claspers.



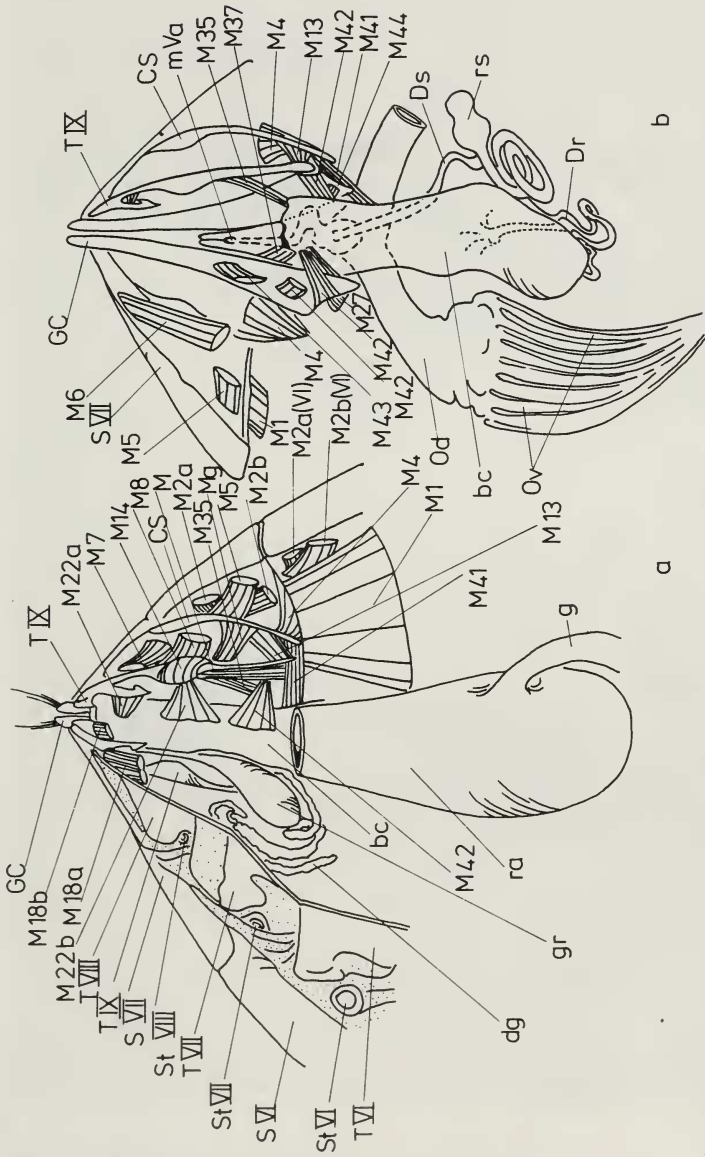


Fig. 8. *Copelatus haemorrhoidalis* (F.), dorsal view of the last segments of abdomen and female genitalia. a. sclerites, muscular system and defense gland, end of rectal ampulla removed. b. muscles of genital appendages and inner genital organs. Legend: bc - bursa copulatrix; CS - gonocoxosterna; dg - defense gland; Dr - ductus receptaculi; Ds - ductus seminalis; g - gut; GC - gonocoxa; GH VIII - genital appendages of segment VIII (l. gonapophysis); gr - reservoir of defense gland; M - muscular system - muscles - of the abdominal segments and female genitalia; mVa - mouth of vagina; Od - oviduct; Ov - ovarium; ra - rectal ampulla; rs - receptaculum seminis; S VI, S VII - sternites of segment VI and VII; St VI - VIII - stigmata of segment VI to VIII; T VI - T VIII - tergites of segment VI to VIII; T IX - tergum IX divided in two lateral claspers. (correction M g = M 9).

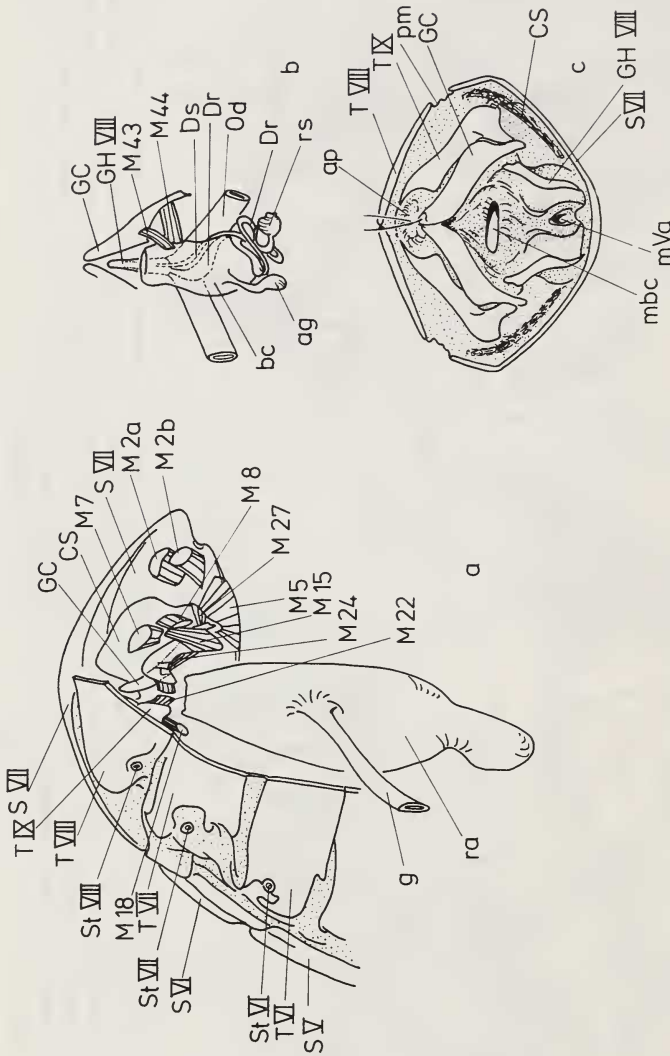


Fig. 9. *Hygrobia tarda* (Herbst), female genitalia. a. dorsal view of the tip of the female abdomen and the muscular system of female genitalia and appendages. b. dorsal view of inner genital organs. c. view of the tip of the abdomen, from posterior aspect, showing the genital appendages and the two openings of the genital ducts in a position before copulation - the gonocoxites are covered by membranes. Legend: ag - accessory gland; ap - anal papilla; bc - bursa copulatrix; CS - gonocoxosterna; Dr - ductus receptaculi; Ds - ductus seminalis; g - gut; GC - gonocoxa; GH VIII - genital appendages of segment VIII (1. gonapophysis); M - muscular system - muscles - of the abdominal segments and female genitalia; mbc - mouth of bursa copulatrix; mVa - mouth of vagina; Od - oviduct; pm - membrane of pleural area; ra - rectal ampulla; rs - receptaculum seminis; S V - S VII - sternites of segment V to VII; St VI - VIII - stigmata of segments VI to VIII; T VI - T VIII - tergites of segment VI to VIII; T IX - tergum IX divided in two lateral claspers.

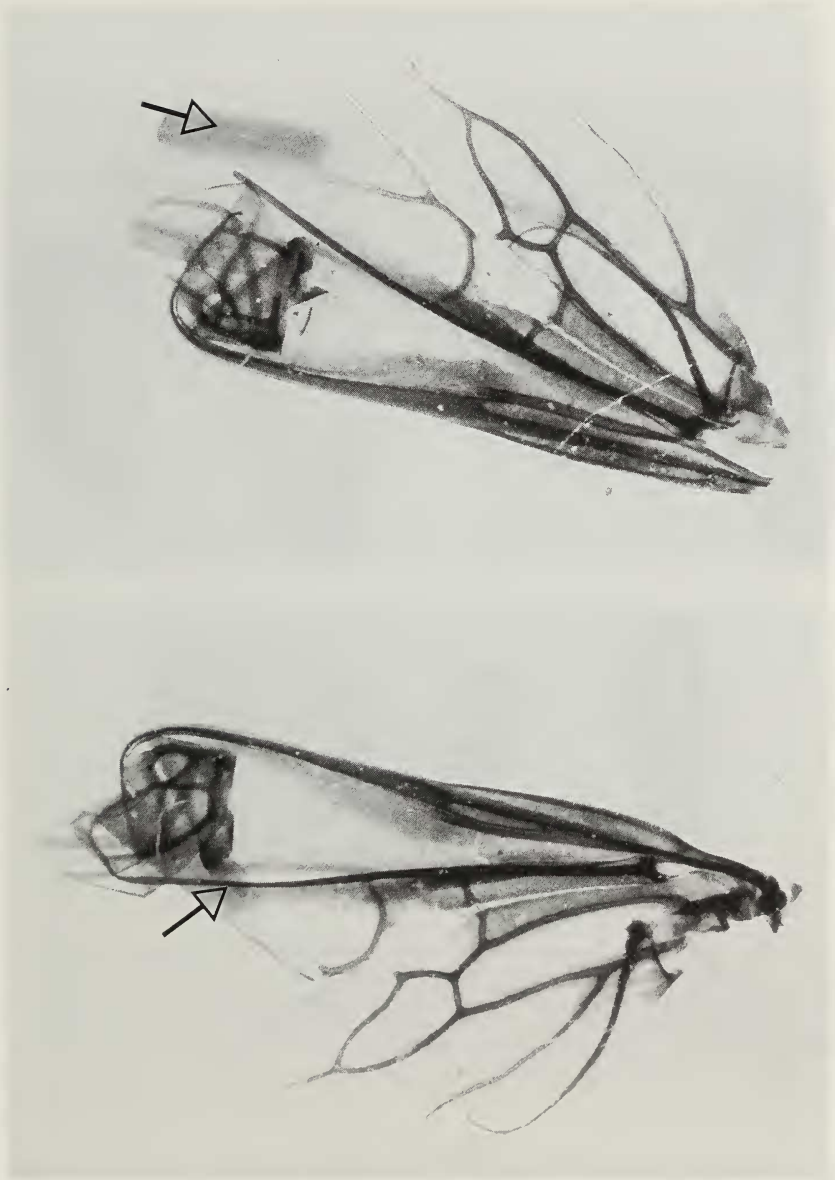


Fig. 10. Folded wings of a. *Amphizoa lecontei* Matthews, Amphizoidae. b. the arrow indicates the area of setal patches or sub-cubital binding patches.



Fig. 11. Inner view of left elytron in different species of Hydradephaga. a. *Amphizoa lecontei* Matthews, Amphizoidae. b. *Agabus bipustulatus* (L.), Dytiscidae. c. *Hygrobia tarda* (Herbst), Hygrobiidae. d. *Hygrobia nigra* (Clark), Hygrobiidae. e. *Copelatus haemorrhoidalis* (F.), Dytiscidae. f. *Noterus clavicornis* (DeGeer), Noteridae. g. *Haliplus lineatocollis* Marsham, Haliplidae. h. *Gyrinus substriatus* Stephens, Gyrinidae.